SIZE DISTRIBUTION, EROSIVE ACTIVITIES, AND GROSS METABOLIC EFFICIENCY OF THE MARINE INTERTIDAL SNAILS, LITTORINA PLANAXIS AND L. SCUTULATA [1,2]

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The two common representatives in Southern California of the nearly worldwide genus, *Littorina,* are *L. planaxis* and *L. scutulata.* The former generally occurs at higher levels in the intertidal, but the zones of distribution of the two species overlap. *L. planaxis* may often be found 5 to 10 feet above spring high tide level, but *L. scutulata* prefers a zone two or three feet on either side of the high tide mark. Published information concerning these two species of snail is scanty in spite of their great abundance and their availability. Their importance to the high intertidal community, however, warrants an extensive study of their ecology, and the present paper describes some of the basic biology of these interesting animals.

Size Distribution

Inspection of colonies of *Littorina* at different places along the La Jolla shore has revealed that the majority of snails at any given locality fall within certain rather well defined size limits. Lysaght (1941) noted a similar condition in *L. neritoides* on the Plymouth Breakwater. In order to gain a more exact picture of size distributions in the present study, three typical *Littorina* environments were chosen, and height measurements were made of all the periwinkles found within a selected area, representative of the environment.

Environmental description

The three environments are shown in Figure 1. The first (Fig. 1a) is a group of pools at Whale View Point in La Jolla. The area is subjected to vigorous wave action at even moderate tides. The second environment (Fig. 1b) is the seaward edge of the top of a broad shelf of rock that extends out from a cliff about 1/4 mile north of the Scripps Institution of Oceanography. The top of Shelf Rock is 1 to $1\frac{1}{2}$ meters above spring tides, but the area under discussion is well splashed at high tide and a large wave may occasionally wash over it. The

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third environment (Fig. 1c) is a protected portion of Shelf Rock some three meters removed from the second environment and splashed only occasionally by large waves.

All three localities are sedimentary sandstone, but the grain size is much finer at Shelf Rock. By exerting pressure the point of a knife may be forced into

FIGURE 1. Photographs of the three environments studied. *a.* Whale View Point; arrow points to typical tidepool from which snails were gathered. *b.* Pools of Shelf Rock; arrow points to region studied. *c.* Dry area of Shelf Rock; Region studied enclosed by white line and marked with arrow labeled 3: arrow labeled 2 points to second environment, about 3 meters away.

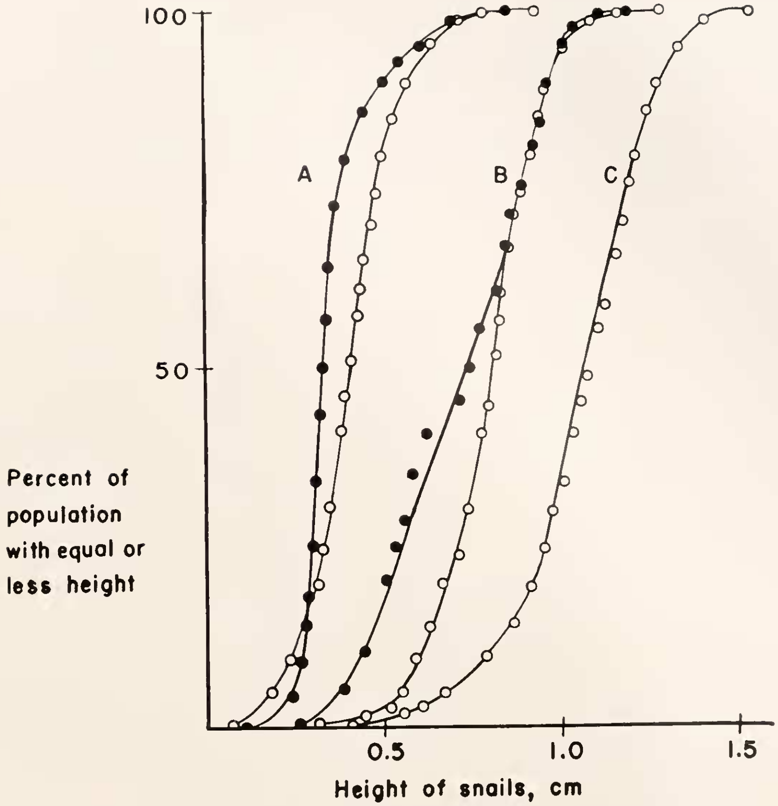

FIGURE 2. Cumulative curves for the *Littorina planaxis* populations of three environments. A. Whale View Point; B. Shelf Rock pools; C. Dry area, Shelf Rock. Measurements made in August, 1951, shown as circles; measurements made in July, 1953 shown as dots.

the sandstones to a depth of about half an inch. The top layers of sand particles may easily be removed by scraping. The topography is characteristically very irregular, great numbers of pools, depressions, basins, and small holes being present.

Results of measurements

The size distribution of *L. planaxis* and *L. scutulata* in each of these environments is shown by means of cumulative curves in Figures 2 and 3. The greatest dimension, "height," was measured, being the distance from the tip of the spire to the lower lip of the aperture. It can be seen that the populations at Whale View Point are rather small, averaging about 0.4 cm. The snails in the pools of Shelf Rock are generally intermediate in size, approximately 0.8 cm., while those on the sheltered dry area of Shelf Rock, although more heterogeneous than the other groups, are generally the largest, averaging almost 1.1 cm. in height. In the latter environment there were insufficient numbers of *L. scutulata* to enable the construction of a reliable curve.

In attempting to explain the variation in size distribution with locality, two possibilities suggest themselves. A favorable set of spawn in different areas at different times, for example, would produce curves of the type that have been obtained. Equally plausible is the contingency that some factor or factors operate in the environment to produce selection for a particular size of periwinkle. If the first hypothesis is correct, curves obtained from measurements made at a later date should be shifted towards the right along the abscissa; that is, effects of growth should be evident. If the latter hypothesis is the proper explanation for the phenomenon, the position on the abscissa of a curve should remain constant with time. Figures 2 and 3 show cumulative curves for populations in the first and second environments, constructed from measurements made about two years after the data discussed above were obtained. Measurements were not attempted for the third environment as appreciable numbers of large periwinkles had been permanently removed from this locality for other experiments. The expected

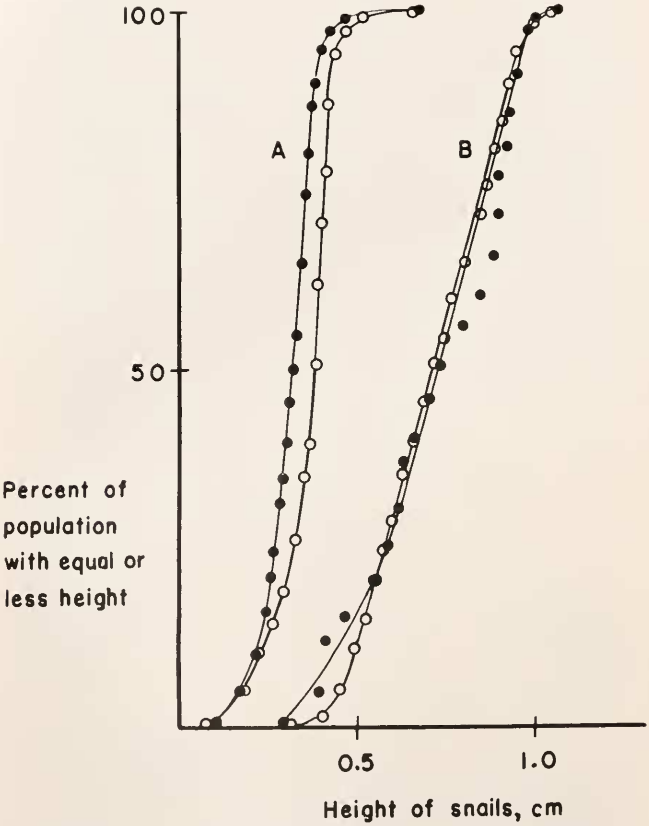

FIGURE 3. Cumulative curves for the *Littorina scutulata* populations of two environments. A. Whale View Point; B. Shelf Rock pools. Measurements made in August, 1951, shown as circles; measurements made in July, 1953, shown as dots.

height increase of *L. planaxis* during this time can be calculated from data given below, and would be of the order of 0.5 cm., but the two sets of curves occupy approximately the same position. Environmental factors, therefore, appear to determine the size distribution of snail populations at any particular locale.

It should be mentioned that the three environments were under constant observation over the period that intervened between the measurements of Figures 2 and 3. The populations were never noticeably different in their size distribution during this time.

Factors affecting size

Wave action and salinity may be among environmental mechanisms capable of causing selection for a given snail size. In many places these two factors are inversely correlated. The higher levels of the spray zone are not wetted by the ocean so frequently as are the lower levels, and have therefore more opportunity for undergoing evaporation and achieving correspondingly greater salinities. The water of the pools and the surface moisture films of the lower levels, on the other hand, are renewed often by waves, and salinities at these localities are therefore not elevated.

As already noted, the three environments studied are subjected to different degrees of wave action. The snail populations composed of larger individuals appear to occupy the drier areas of the spray zone. In order to determine whether water currents might be more effective in removing large than small snails the following experiments were performed.

Four small (approx. 0.6 cm.), four intermediate (0.9–1.2 cm.), and four large (1.4–1.6 cm.) specimens of *L. planaxis* were placed on a small flat rock in a tidepool. When all the snails had emerged from their shells and were observed creeping, the rock was moved rapidly through the pool, creating a water current across the shells. After several vigorous swings through the water, only three small snails were left. A repetition of the experiment using six small, four intermediate, and four large snails ended with only four small snails remaining attached to the rock. When twelve medium-size *L. scutulata* (approx. 0.9 cm.) were placed on the stone with three small and two large *L. planaxis* for comparison purposes, the large specimens of the latter species were washed off with relative ease. After much effort three of the *L. scutulata* were eventually swept away, leaving nine of this species and the three small *L. planaxis* when the experiment was discontinued.

When a stream of sea water from a hose was allowed to play against the shells of *L. planaxis* creeping on a flat rock, large individuals were washed off more readily than small ones, and a snail of a given size was removed with greater ease when the stream was directed against the posterior part of the shell.

In order to gain an idea of the current velocities necessary to dislodge a snail, specimens of *L. planaxis* were placed in a Plexiglass tube of 3.5 cm., inside diameter, and after the animals had emerged from their shells and were crawling on the surface of the Plexiglass, the tube was gently filled with sea water. A current of known velocity was then allowed to flow through the tube and notations were made of the ability of the snails to remain attached for 10 seconds. The results are given in Table I. A total of 10 large and 8 small snails was used in the experiment, and 6 trials were conducted.

Several hypotheses offer plausible explanations for the ability of small *L. planaxis* to withstand currents that remove large individuals. Physical factors might include greater water friction acting as drag on larger shells, or frictional forces slowing the current in the vicinity of the rock-water interface[3] thus favoring smaller snails. Biological factors might include loss of vigor and of tenacity with increasing age, or a disproportionate growth of the various parts such that the sole of the foot does not increase as rapidly as the surface area of the shell. Figure 4 shows that the last hypothesis is not supportable, hence one or more of the other factors may contribute to the distribution phenomenon.

TABLE I

Effect of current velocity on two size groups of Littorina planaxis

Size group	Velocity of current flowing over snails meters/second	Fraction of snails removed by current per cent
Large snails	3.4	90
(1.3 to 1.6 cm.)	2.3	90
	2.0	80
Small snails	3.4	50
(approx. 0.7 cm.)	2.0	50

The absence of large snails from areas exposed to vigorous wave action may thus be explained, but account has not yet been taken of the absence of small snails in the high, dry areas of the spray zone. The solution to this problem may lie in physiological age changes rendering the animal more capable of coping with exposure to air or to more variable salinity conditions. Salinity has been shown to influence shell size and shape in *Littorina* (Thorson, 1946; Agersborg, 1927) and further study along these lines will be necessary before a complete explanation of the observed size distribution can be proposed.

EROSIVE ACTIVITIES

Many intertidal animals bring about erosion of rock. *Littorina* species often occur in small basins above high water mark (Fischer-Piette, 1932; Clench, 1938; Lysaght, 1941) and have been credited by some investigators (Brunelli, 1928; Welch, 1929) with the production of depressions in rock. The snails feed by applying a file-like ribbon, the radula, to the substratum and transfer bits of it to the mouth by a scraping action. On the cliffs around La Jolla the animals scrape algae and fine detritus from the rocks and at the same time remove particles of the rock itself. Because of their great abundance, erosion resulting from their feeding is believed to be appreciable, and a quantitative estimation of the magnitude of the erosion will be useful in determining its importance with respect to other erosive processes.

Since the animals may not behave as they do in nature when kept in the laboratory over long periods of time, it seemed wisest to obtain as much data

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[3] An idea for which I am indebted to Professor Roger R. Revelle.

as possible from snails in their normal environment. The simplest means for accomplishing this appeared to be to determine the number of times daily the gut contents are completely renewed, and also the proportion of the gut contents that is inorganic matter. The product of the two quantities would yield the daily rate of erosion.

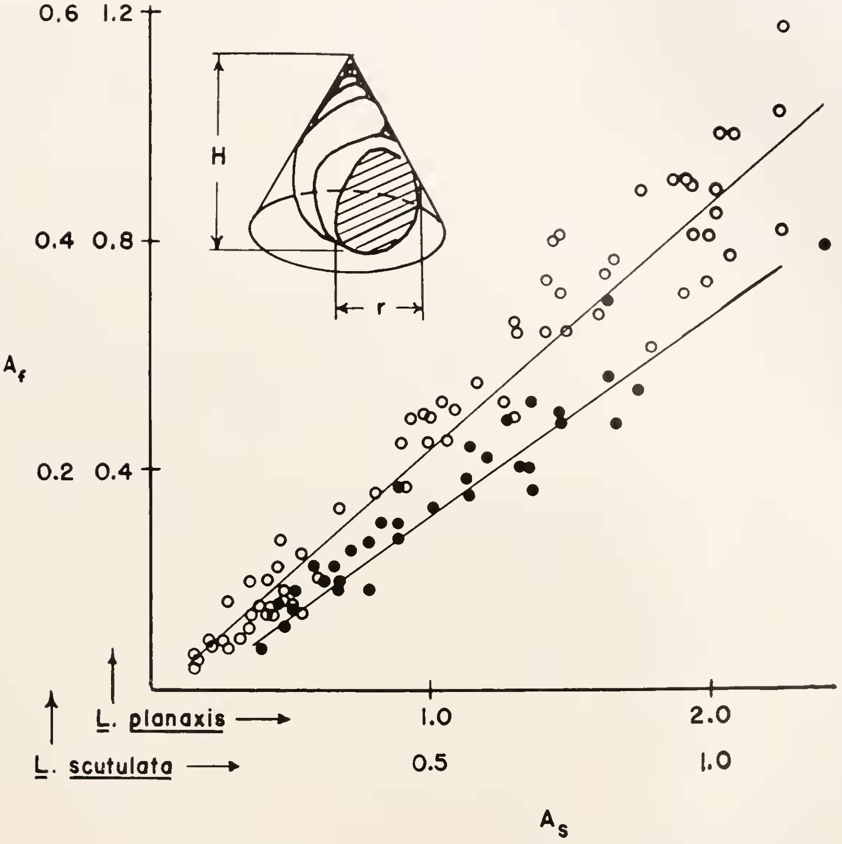

FIGURE 4. Relationship of shell surface to surface of the sole of the foot for *Littorina planaxis* and *L. scutulata,* indicating that the increase in area of each with age is proportionately the same. The sole area (A_f) was measured while the animals were crawling up the sides of a glass vessel. Shell surface (A_s) was arbitrarily taken as $1/\pi$ of $\pi \sqrt{r^2 + H^2}$, the formula for the curved surface of a right cone.

Time required to renew material in the gut

The number of times daily the gut contents are renewed will depend on the rate at which material is passed along the gut, which in turn may vary with the amount of time the snail is able to feed. Dissection of specimens of *L. planaxis* taken both from pools (46 specimens) and from areas that become dry at low tides (30 specimens) revealed that throughout the day the intestines of the former group were always full of unconsolidated material, whereas the intestines of the latter

TABLE II

Summary of an experiment to determine the time required for Littorina to cycle food completely through the gut; May 18, 1953; water temperature range 17° to 30° C.; 20 snails per size group

Species	Height cm.	Time elapsed until		
		First blue fecal pellet observed, hr.	Half of group defecated blue feces, hr.	Entire group defecated blue feces, hr.
L. planaxis	0.4–0.5	$1\frac{2}{3}$	2	3
L. planaxis	0.7–0.95	2	$3\frac{3}{4}$	5
L. planaxis	1.3–1.6	$2\frac{1}{2}$	$4\frac{2}{3}$	–*
L. scutulata	0.3–0.45	$1\frac{2}{3}$	2	3
L. scutulata	0.8–0.95	$2\frac{1}{3}$	4	5

* Thirteen had defecated blue feces after $7\frac{1}{2}$ hours.

group were generally at least partially full but sometimes almost empty. It was concluded that animals in the pools graze sufficiently to keep the gut full at all times. Snails feeding on areas that become dry at low tide appear to graze only when the surface is moist, and the amount of material in the gut consequently is variable.

In order to determine the rate at which material is passed through the gut, groups of snails were allowed to graze on a section of Shelf Rock stained with the

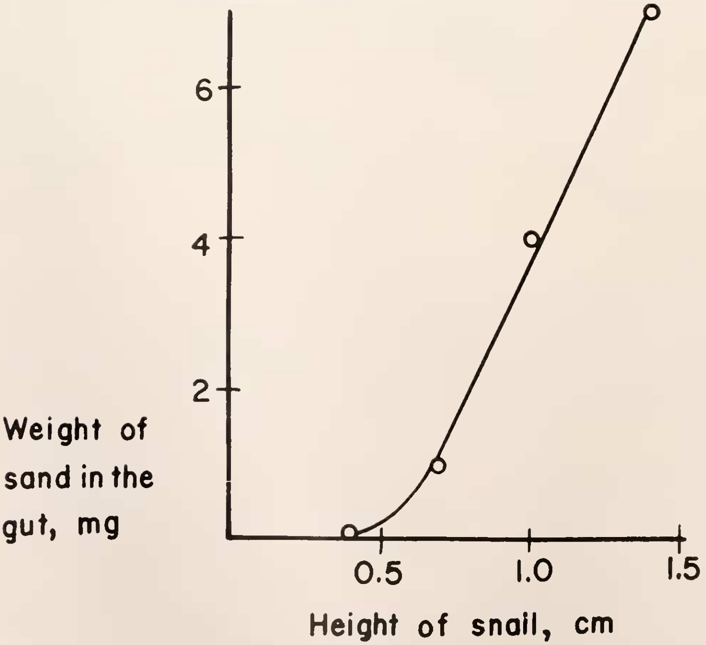

FIGURE 5. Relationship of sand contained in the gut to height of *Littorina planaxis*.

harmless dye methylene blue. After a period of an hour and a half had elapsed, the animals were removed to an unstained area and carefully observed for the first appearance of blue fecal pellets. While they were on the stained and unstained rock, the periwinkles were washed with fresh sea water every 10 minutes, and their behavior during the experiment seemed normal. Five such experiments were conducted on two spring and on three summer days. For snails of height 0.8 cm., cycling times of 2½ to 6 hours were obtained. The results were always similar and are described in Table II for one of the experiments.

A typical 0.8-cm. snail in a Shelf Rock pool, therefore, feeds sufficiently to keep the gut full at all times and probably renews the material completely four to eight times daily.

Inorganic matter in the gut

Sand in the gut was determined by extracting snails from their shells, incinerating the bodies in a tared crucible, cooling, adding a little concentrated hydrochloric acid to dissolve body ash, carefully decanting, rinsing, re-incinerating and weighing. Four size groups of 50 *L. planaxis* each were thus analyzed and the results are presented in the curve of Figure 5. An 0.8-cm. snail therefore contains on the average about 1.6 mg. of sand in the gut.

Calculated rate of erosion

Taking the Shelf Rock region, and considering the simplest case of a snail feeding in a pool, an estimation of erosion may now be made. It has been shown (Fig. 2) that the population in this environment averages 0.8 cm. in height. The average amount of inorganic material contained in the gut of an 0.8-cm. snail was found to be 1.6 mg., and, if we take the most conservative cycling period of 4 times daily, we obtain the value of $1.6 \times 4 = 6.4$ mg. of inorganic material passing through the gut of the snail per day. This presumably is equivalent to the amount of rock eroded daily. The density of Shelf Rock is approximately 2.5 g./cc. and calculations show that 100 snails, 0.8 cm. in height, would be capable of excavating a basin of 86 cc. yearly, almost a liter in a decade.

The concentration of *L. planaxis* in the environment under discussion is of the order of one snail per 30 cm.^2 Erosion by this species alone, therefore, may be calculated to deepen the pools one cm. every 40 years. If *L. scutulata* is considered, the snail concentration increases to one snail per 12 cm.^2, and assuming that 0.8-cm. individuals of both species have similar feeding rates and weight of gut contents, erosion by both *Littorina* species combined will deepen the pools one cm. every 16 years. The snail concentration has remained fairly constant over the two-year period that is covered by these observations.

Comparison with erosion from other sources

Other erosive processes acting on the sandstone rocks of this area have been studied by Emery (1941, 1946). For exposed surfaces a general erosion rate of one cm. every 20 years was estimated, while for pools at Whale View Point nocturnal pH changes at low tides were calculated to cause a deepening of the pools by one cm. every 33 years. The different processes causing rock erosion are probably additive in some cases and in other instances facilitate each other and are not additive.

GROSS EFFICIENCY

The average, gross metabolic efficiency, or the ratio of ingested food to organic matter incorporated as living tissue, may now be estimated for *L. planaxis* with the aid of additional data that have been obtained.

Growth

Growth rates were determined by measuring the increases in height of marked specimens of *L. planaxis* on Shelf Rock at various intervals for a period of a year and a quarter. The methods of converting an increase in spiral length to a height increase, used by Moore (1937) and Lenderking (1951) with other littorines, seemed to be complicated in the present case, since the apex angle of *L. planaxis* varies considerably, and it therefore appeared simplest to measure height increments over a long period of time. Figure 6 illustrates the results of the experiment, showing the growths of positively identified individuals from the snails that were recovered, out of a total of 300 originally marked. It may be noted that an 0.8-cm. snail has an average height increment of about 0.02 cm. per month.

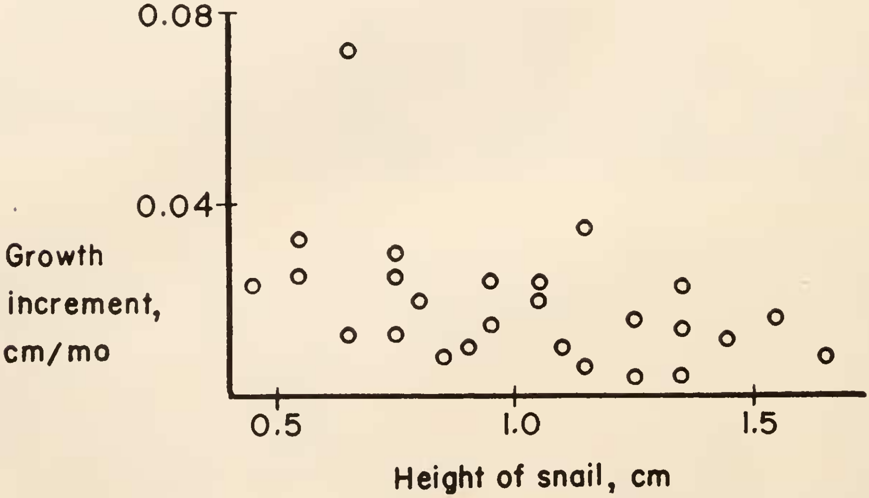

FIGURE 6. Twenty-six monthly growth increments observed in specimens of *Littorina planaxis* at Shelf Rock.

To convert this value to an increase in tissue weight the relationship between snail height and dry tissue weight was obtained and is shown in Figure 7. Specimens of *L. planaxis* were dried in a vacuum oven for 24 hours at 80° C. and 460 mm. pressure. After cooling in a desiccator, the shell and dry tissue were weighed and the shell weight was obtained after removing the dry tissue by a half hour's immersion in boiling 20% KOH. Dry tissue weight was then readily calculated

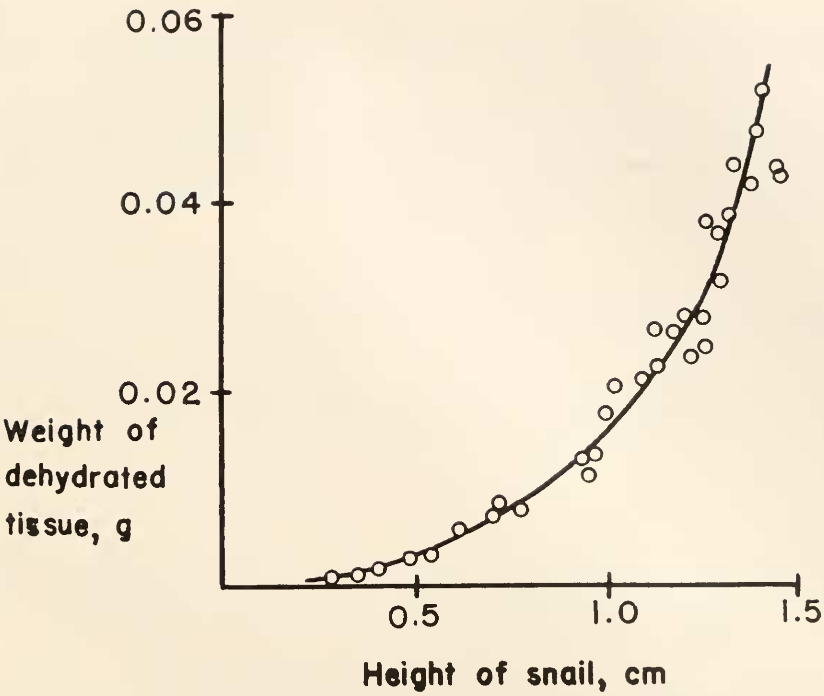

FIGURE 7. Relationship between dry tissue weight of *Littorina planaxis* and height.

by subtraction. Computations using Figure 7 indicate that an 0.8-cm. snail growing 0.02 cm. per month would have an increase in dry weight of 0.6 mg. for a like period.

Ingestion of organic matter

Determination of the amount of food ingested monthly could be readily accomplished if the organic matter per cent of the material swallowed by the snail were known. In scraping the surface of rocks, however, the snail has an excellent

TABLE III

Organic content of various materials

Material analyzed	Organic matter per cent	Average
Snail feces	2.4	
	2.0	
	3.0	
	3.2	2.7
Light manual knife scrapings of rock surface	2.4	
	2.6	2.5
Loose sand from tidepool bottom	0.8	
	1.0	0.9

mechanism for removing only a thin, organic-rich layer of material. Even the lightest of scrapings made by a knife might remove much underlying rock along with the surface "skin" of organic matter. To estimate the organic matter per cent of the material swallowed by the snail, therefore, it seemed best to assume that only a small fraction of the organic molecules will be assimilated through the gut wall, and that the feces would therefore have approximately (and conservatively) the same organic content as the ingested material. Corrections for this assumption can then be made and the efficiency recalculated.

Fresh snail feces may easily be obtained in abundance, and the results of organic analyses on these and other materials by Walkley and Black's rapid titration method (chromic acid digestion) are given in Table III.

It was found in calculating erosion that an 0.8-cm. snail voids 6.4 mg. of inorganic material daily and this amounts to 192 mg. per 30-day month. If the feces are 2.7% organic matter the amount of organic material voided per month is 5.3 mg. Making use of the assumption explained above, this is approximately equal to the monthly ingested organic matter.

Calculation of gross efficiency

For an 0.8-cm. snail in the pools of Shelf Rock the gross efficiency may now be estimated as $\frac{\text{Organic matter added as tissue}}{\text{Organic matter ingested}} \times 100$ which equals $\frac{0.6}{5.3} \times 100 = 11\%$.

In order to refine the calculation let us consider how much of the ingested organic matter might reasonably be assimilated across the gut wall from the food, of which some is built into new tissue. There must also have been assimilated a sufficient quantity of material to account for organic matter lost in respiration, and since the animals are poikilothermic and slow in movement, it would seem that this loss should be less than 4 times the amount added as new tissue. Taking the latter, then, as 20% of the total assimilated, and all other losses combined as 80%, and knowing that the animal adds 0.6 mg. per month as new tissue, we have 3 mg. per month as an estimate of the amount of organic matter assimilated across the gut wall. Recalculating the efficiency gives a value of $\frac{0.6}{5.3 + 3.0} \times 100 = 7\%$.

It will be recalled that in calculating erosion the time for cycling food through the gut was taken conservatively as 6 hours. The average value might be less, which would increase the erosion rate and depress the efficiency.

SUMMARY

1. Size distribution curves for populations of the marine intertidal snails *Littorina planaxis* and *L. scutulata* in three environments are presented.

2. It is concluded that environmental factors cause the observed size distributions, and the amount of wave action at a given locale appears to be one of the influencing factors. *L. planaxis* was observed to cling to a smooth surface in current velocities of two to three meters per second for 10 seconds.

3. The time for littorines to cycle food completely through the gut varied with size. Snails 0.8 cm. in height required from 2½ to 6 hours.

4. Erosion resulting from the snails' feeding activities was estimated for certain tidepools and found to deepen tidepools one cm. every 16 years. This is of the same order of magnitude as other erosive processes which have been studied in the same region.

5. Growth of *L. planaxis* was found to average 0.02 cm. per month in height increment, and 0.6 mg. per month in dry weight of organic matter.

6. The gross metabolic efficiency was computed and is estimated to be in the neighborhood of 7%.

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